

THE EVOLUTION, HOST RELATIONSHIPS AND
CLASSIFICATION OF THE NEMATODE
SUPERFAMILY HETERAKOIDEA



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By WILLIAM G. INGLIS

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APOLOGIA

SEVERAL years ago I published a classification of the nematode Superfamily Heterakoidea (Inglis, 1958) but presented no justification as I always hoped to produce a full revision. It has become increasingly clear that this is never likely to be completed largely because of a shift in my interests in conjunction with a lack of material on which to base such a revision. I therefore present here reasons for the classification previously proposed and regret being unable to complete the whole work. No illustrations are given as they can be found in Skrjabin, Schikhobalova and Lagodovskaja (1961) and Chabaud (1965).

SYNOPSIS

The comparative anatomy of the Superfamily Heterakoidea is described and the morphological sequences recognized are used as the basis for the classification proposed. The evolution of the superfamily is interpreted in terms of (1) intra-host localisation; (2) major host groups (i.e. amphibia, reptiles, birds and mammals); (3) the feeding habits and ecology of the hosts; and (4) geographical restriction. The superfamily is classified into three families, five subfamilies and fourteen genera, thus: Heterakidae: Heterakinae (*Heterakis*, *Odontoterakis*, *Pseudaspidodera*); Meteterakinae (*Meteterakis*, *Giveterakis*); and Spinicaudinae (*Spinicauda*, *Africana*, *Moaciria*, *Strongyluris*). Aspidoderidae: Aspidoderinae (*Aspidodera*, *Ansiruptodera*); and Lauroiinae (*Lauroia*, *Paraspidodera*). Ascaridiidae (*Ascaridia*). A key is given to the genera of the superfamily. The following genera are not accepted largely because the morphology of the specimens does not correspond to the published descriptions, thus: *Preterakis* Freitas, 1956; *Heterakoides* Freitas, 1956; *Paraterakis* Freitas, 1956; *Pseudaspidoderoides* Freitas, 1956; *Pseudaspidoderina* Freitas, 1956; *Raillietakis* Freitas, 1956; *Sexansodera* Skrjabin & Schikhobalova, 1947; *Bellaplectana* Skrjabin, Schikhobalova & Lagodovskaja, 1961; *Spinaspidodera* Skrjabin & Schikhobalova, 1947; *Ganguleterakis* Lane, 1914; and *Cheloniheterakis* Yamaguti, 1961.

INTRODUCTION

No full revision of the Heterakoidea or Heterakidae has ever been carried out although several groupings have been proposed largely based on other published work. However, Travassos (1913) did produce a partial revision based largely on the species occurring in Brazil. Other minor changes in the classification were proposed later but no major alterations were suggested for almost thirty-five years when Skrjabin & Schikhobalova (1947, 1947a), Freitas (1956), Inglis (1957, 1958) and Chabaud (1957) all advanced new groupings. Most recently the superfamily has been re-grouped once more by Skrjabin, Schikhobalova & Lagodovskaja (1961) and by Yamaguti (1961).

All the classifications proposed, except my own, have been based on biblio-taxonomic studies while the results presented here are based on a study of virtually all the type material available in the world's collections together with a study of many other specimens.

In anticipation of the discussion that follows it may be stressed that the following genera proposed by Freitas (1956) and Skrjabin *et al.* (1961) cannot stand because the descriptions they classify are contradicted by the morphology of the specimens, thus: *Bellaplectana* Skrjabin *et al.*, 1961 is a synonym of *Moaciria* since *Aplectana pharyngeodentata* Belle, 1957 (of which I have studied the type series) does not

possess the so-called teeth in the buccal cavity on which the genus is based. These structures are simply the retracted lips, a common artefact in poorly preserved *Spinicauda* and *Moaciria* species. *Preterakis* Freitas, 1956 falls as a synonym of *Africana* because the fusion of the caudal alae on the male tail on which it is based does not occur. Such an apparent fusion occurs in many specimens of the superfamily but is an artefact due to contraction during fixation and even the artefact does not occur in all the specimens of the type series of *Africana astylosterni* Sandground, 1933. As a consequence the subfamily Preterakinae Freitas, 1956 must also disappear.

Finally the following genera proposed by Freitas (1956) are not accepted by Skrjabin *et al.* (1961) nor by myself, thus: *Heterakoides* Freitas, 1956 since, although *Spinicauda triaculeatus* Kreis, 1933 is certainly slightly different from the other species referred to *Meteterakis* (Inglis, 1958a) I still do not feel it warrants generic separation. Similarly the genus *Pareterakis* Freitas, 1956 is a synonym of *Meteterakis* since there are no characters which allow it to be distinguished. *Pseudaspidoderoides* falls because the anastomosing cordons reported by Chakravarty (1938) appear to be due to contraction of the type specimens, which I have seen.

COMPARATIVE ANATOMY OF THE SUPERFAMILY

All the species referable to the Superfamily, with the exception of the genera *Ascaridia* and *Lauroia* which are discussed later, have the following features in common. The head bears three large, distinct lips, the detailed structure of which varies throughout the family and has been considered elsewhere (Inglis, 1957). In summary, however, the dorsal lip carries two doubled papillae and each ventro-lateral lip carries a single ventro-lateral doubled papilla and a single lateral papilla associated with the amphid. The inner surface of each lip carries an anterior flange which varies in relative size throughout the superfamily. The head in *Lauroia*, which I did not deal with before, is typical of this pattern with lobes connecting the lips. It is, however, characterized by the development of three plate-like regions posterior to each lip. This is clearly a development of cordons from one source (see particularly Proença's (1938) figures of *L. travassosi*) comparable to the condition in *Gireterakis*. In *Ascaridia* the lips are large and stout but otherwise typically Heterakoid.

The anterior region of the oesophagus is divided into three separate anterior lobes, previously called "pharyngeal portions", at the tip of each of which is a cuticular onchium, except in one case. From studies completed since 1957 it now appears that the lips are operated by a system of fibres which are not arranged in a septum as in the Ascaridoidea (Inglis, 1965) but this has not been fully analysed. In addition in the Heterakinae there is generally a pair of lateral papillae lying on the body just posterior to the lip region.

The oesophagus, except in *Ascaridia*, is modified anteriorly into a short region generally called a pharynx and swells fairly evenly posteriorly to form a bulb-like region, containing three valves, which is not clearly offset from the remainder of the oesophagus by a constriction. The distinction between the pharyngeal region, the bulb and the remainder of the oesophagus is the presence of marginal tubes

in the radii of the lumen of the oesophagus in the intervening length between the bulb and pharynx. Into these marginal tubes project a series of paired leaf-like cuticular structures and this arrangement gives the oesophagus its typical longitudinal doubled appearance.

The oesophagus is relatively long and narrow with a markedly small posterior bulb in *Aspidodera*, *Anisruptodera*, *Lauroia* and *Paraspidodera*; the oesophagus is less markedly narrow in *Africana*, *Gireterakis*, *Meteterakis*, *Moaciria*, *Spinicauda* and *Strongyluris*, and is relatively short and stout in *Heterakis*, *Odontoterakis*, and *Pseudaspidodera*. The oesophagus is club-shaped without a posterior bulb in *Ascaridia*. The nuclei of the ventral oesophageal glands are doubled.

Lateral alae, which may be prominent in the cervical region, are typically present. They are relatively broad in *Heterakis*, *Odontoterakis*, *Pseudaspidodera* and *Gireterakis*; are present but relatively narrow in *Africana*, *Spinicauda*, *Moaciria* and *Strongyluris*—in which genera the lateral fields are very prominent—and also in *Meteterakis* and *Ascaridia* but they are lacking in *Aspidodera*, *Anisruptodera*, *Lauroia* and *Paraspidodera*.

The nerve ring encircles the oesophagus about one third of its length posterior to the pharynx and the excretory pore opens just posterior to the nerve ring.

Small sessile papillae are borne on the general body surface in *Africana* (few), *Meteterakis* (few), *Spinicauda* (very few), *Moaciria* (many) and *Strongyluris* (many). Such papillae are, however, frequently difficult to see and they are probably more easily seen in *Strongyluris* species because such species are relatively larger than the others.

The Male Tail

A circular pre-cloacal sucker with a cuticular rim is always present (except in *Lauroia*). Caudal alae are fairly common in the superfamily and, when present, never meet on the ventral surface of the body anterior to the pre-cloacal sucker. In those specimens in which the tail has contracted during fixation such a junction may appear to exist but it is clearly an artefact and is, therefore, of no use as a systematic character. Freitas (1956) lays considerable stress on this "junction" of the caudal alae, going so far as to use it to differentiate genera. I would stress that not only is this an artefact but it is not present in all the specimens of most of the species of which it is considered a diagnostic character.

In the genera *Heterakis*, *Odontoterakis* and *Pseudaspidodera* there are, typically, eleven pairs of caudal papillae, of which seven pairs are long and support broad caudal alae. Two pairs of these papillae, which are always slim, flank the pre-cloacal sucker, four pairs lie lateral to the cloacal opening (later referred to as the para-cloacal papillae), and one pair lies posterior to the cloacal opening, roughly midway between the para-cloacals and the terminal spike of the tail. The remaining four pairs of papillae are typically sessile, two pairs flank the cloacal opening, the peri-cloacal papillae, of which one pair is pre-cloacal and one pair post-cloacal. The remaining two pairs of papillae lie at the base of the terminal spike of the tail with one pair wholly ventral and one pair lateral in position. The phasmids open just anterior to the terminal group of ventral papillae and have generally been

described as papillae. In some cases additional papillae occur, in particular a pair of sessile papillae frequently occur anterior to the suctorial pairs and an additional long pair sometimes occurs immediately posterior to the para-cloacals.

The tail ends posteriorly in a long, narrow, evenly pointed, non-alate terminal spike. In all four genera the pre-cloacal sucker is relatively large and there is no gubernaculum.

Both *Spinicauda* and *Africana* have long narrow tails bearing many small sessile papillae and a relatively small pre-cloacal sucker. There are no caudal alae in *Spinicauda* while those in *Africana* stop posteriorly at the level of the cloacal opening and are unsupported by papillae. A gubernaculum is present in *Spinicauda* and a gubernacular mass in *Africana* (gubernacular mass is a term proposed earlier for the strongly cuticularized lining of the cloaca in the genus *Meteterakis* (Inglis, 1958a)).

The tail in *Strongyluris* is very short with a large pre-cloacal sucker which is directed posteriorly. The caudal alae are very broad and are typically supported by seven pairs of long stout papillae of which the largest are the three most anterior pairs, with the others becoming increasingly smaller posteriorly. There are, in addition, two pairs of ventral sessile papillae peri-cloacal in position and one similar pair just anterior to the beginning of the terminal spike. There is no gubernaculum. The tail in *Moaciria* is similar but with a long terminal spike and a gubernaculum.

The relatively long, narrow tail in *Meteterakis* is characterized by a small pre-cloacal sucker and narrow caudal alae supported by, typically, three, exceptionally four, pairs of short, stout papillae of which, typically two pairs, exceptionally three pairs, lie about the level of the pre-cloacal sucker and the remaining pair is roughly at the level of the cloacal opening. There are in addition many pairs of small sessile papillae (up to about twenty) on the tail which may represent the caudal complement of the similar papillae which are found scattered generally over the surface of the body. A gubernacular mass is present in all except one (possibly two) species. The tail in *Gireterakis* is very similar to that of *Meteterakis* with the same three pairs of swollen papillae supporting the caudal alae but there are much fewer small sessile papillae and there is no gubernacular mass.

The tail in the genera *Aspidodera*, *Ansirutodera*, and *Paraspidodera* is so uniform that one description will cover all three. It is long and thin, tapering evenly to a point. It has no caudal alae, the pre-cloacal sucker is markedly small and there is a large number of small sessile papillae arranged in roughly parallel rows. A gubernaculum is present in all three genera.

The tail in *Lauroia* is highly modified but may be interpreted as being derived from a tail similar to that characteristic of the previous three genera by a great reduction of all its structures. Thus the pre-cloacal sucker is represented by a slight swelling and the number of sessile caudal papillae is very small.

The tail in *Ascaridia* is relatively stout with narrow alae supported by short stout papillae. The pre-cloacal papillae are sessile and there is no gubernaculum.

The Spicules

The spicules are always equal in length, non-alate, simple and identical in structure in the genera *Africana*, *Ascaridia*, *Aspidodera*, *Ansirutodera*, *Moaciria*, *Paraspido-*

dera, *Spinicauda* and *Strongyluris*. They are equal in length and identical in structure, with alae in some cases, in *Meteterakis* and *Africana*. They are equal in length and slightly elaborate although identical in structure in *Gireterakis* while in *Heterakis*, *Odontoterakis* and *Pseudaspidodera* they are frequently unequal in length and may be very dissimilar in *Heterakis* and *Pseudaspidodera* but are always simple, needle-like in *Odontoterakis*. It may be noted here, and will be referred to later, that the general facies of the male tail in *Aspidodera*, *Ansiruoptodera*, and, to a lesser extent, *Paraspidodera* is remarkably uniform even to the same general shape of the spicules which are, almost invariably, rather stout with squarish ends.

SYSTEMATIC GROUPS WITHIN THE SUPERFAMILY

This section should be read in conjunction with the discussion of morphological trends given in the next section, since the classification presented reflects the sequences discussed there. In other words this classification is largely *akoluthic* (sensu Inglis, 1966a) in reflecting trends in morphological modification rather than in attempting to assess over-all resemblances or simply utilizing key characters. It does appear, however that an assessment of over-all resemblances would produce a classification the same as the present since virtually the only characters available for analysis are those of the head and the male tail and a classification based on either alone is congruent with one based on the other. That is, if only tails are classified they fall into roughly the same major groupings as do the heads if classified alone. This explanatory discussion of procedure intrudes here because in classifications such as this I find it impossible to separate the discussion of the process of classification from that of the establishment and recognition of morphological trends. In fact the trends were probably recognized before the classification was developed. It is, however, easier to follow the discussion of trends and host relationships if a foundation is given upon which they can be discussed.

As stressed above most classifications of this superfamily (family) have been mainly based on published descriptions which are in many cases incomplete or inaccurate. A reliable assessment of such descriptions, and the characters upon which to form a classification can only be made after a wide and detailed knowledge of the group under consideration has been obtained. The dangers involved in bibliotaxonomy are exemplified by the gross oversplitting proposed by Freitas (1956) with a multiplicity of new names at all levels of taxa. The classification proposed by Freitas may be considered analytical in that he has given systematic recognition to any differences he found. The classification proposed here is basically synthetic with a stressing of similarities rather than differences although, obviously analysis must precede such a process.

The superfamily contains three morphologically distinct groups which differ in the forms of the lips, of the oesophagus and of the male tail. One is characterized (1) by square lips which are connected by lateral lobes, (2) by a cephalic cap (i.e. a thickening of the cuticle at the anterior end of the body), (3) by a markedly long and narrow oesophagus which expands relatively suddenly into a small posterior trivalvulate oesophageal bulb and (4) by males with relatively long, narrow, evenly pointed tails without alae, typically bearing many small sessile papillae, (5) a

relatively small pre-cloacal sucker, (6) having relatively massive, square ended spicules without alae and (7) possessing a gubernaculum. This group I recognize as the Family Aspidoderidae.

The second group is characterized by (1) rounded lips without lateral lobes, (2) no cephalic cap, (3) a relatively short stout oesophagus which merges rather slowly into a relatively large posterior tri-valvulate bulb and (4) by males in which the tail (with the exception of one genus) always carries caudal alae, (5) the spicules are frequently dissimilar and alate, (6) a gubernaculum is generally lacking, and (7) there is a tendency for the pre-cloacal sucker to be prominent and for the caudal papillae to be large. This group I treat as the Family Heterakidae.

The third group is characterized by (1) massive lips without anterior cuticular flanges or (2) lateral lobes or (3) onchia at the anterior ends of the pharyngeal portions which are themselves very small, (4) the oesophagus is grossly club-shaped without a posterior oesophageal bulb or valvular apparatus, (5) the male tail carries the usual circular pre-cloacal sucker with a definite cuticular rim but, although the papillae are grouped round the region posterior to this sucker, they are generally stout and rounded without marked lateral caudal alae, (6) there are frequently files of sessile papillae running down the lateral sides of the body. This group I treat as the Family Ascaridiidae.

I did not previously accept the Family Ascaridiidae as referable to the Heterakoidea (Inglis, 1958; 1958*b*) and argued that it was Ascaridoid. In this I was clearly wrong. I have now studied the Ascaridoidea (Inglis, 1965, 1965*a*) and am convinced by the overwhelming weight of evidence that the Ascaridiidae are heterakoids and that their resemblances to the Ascaridoidea are simply due to the convergent development of a massive body size. The form of the male tail and the presence of paired nuclei in the ventral oesophageal glands are clear features of resemblance with the Heterakoidea and rule against ascaridoid affinities, as does the life history. Equally significant is the structure of the head which in the Ascaridiidae is heterakoid in plan and shows no point of resemblance with that in the Ascaridoidea, other than gross size. The lips in the Ascaridoidea are operated by a septum of three systems of non-contractile fibres (Inglis, 1965) and the cheilorhabdion (i.e. the cuticle lining the inner surface of the cheilostome: Inglis, 1966, 1967) is never markedly sclerotized. In Ascaridiidae the conditions are quite different. The cheilorhabdion is modified into a definite heavily sclerotized region in each lip while the fibre system, which is present, is not organized as three subsidiary systems but is sparse except in the inter-labial regions from which it fans out into each contiguous lip. Exactly the same occurs in the heterakids and aspidoderids. Further the arcade system and associated cells bears no resemblance to that of the Ascaridoidea (Hartwich, 1957).

I continue to treat the Aspidoderidae as a distinct family in spite of Chabaud (1957; 1965) who considers it a subfamily of the Heterakidae. I did at one time agree with Chabaud over this point but further consideration leads me to conclude that to do this masks the many and manifest differences between the aspidoderids and the heterakids. The forms included within the Aspidoderidae differ in so many features from those referred to the Heterakidae, they form such a specialized,

geographically restricted group and reach such a degree of independent specialization in a form such as *Lauroia*, that I look on them as being as distinct from the Heterakidae as are the Ascaridiidae.

Lauroia is a particularly aberrant genus at first sight and this has led to its being referred to a unique family within a different Superfamily by Skrjabin *et al.* (1961) but I have studied some of the syntype series of *L. travassosi* Proença, 1938 (type species of the genus) and *L. intermedia* Caballero, 1955. The lips have the inter-connecting lobes typical of the aspidoderids and this may be considered a specialized form of the head found in *Paraspidodera*. Further the reduction in the structures of the male tail is so obviously secondary, and has involved all structures, that little stress can be laid on this alone. But in *L. trinidadensis* Cameron, 1939 there is a definite small bump anterior to the pre-cloacal opening which can be considered to be the reduced remnants of a pre-cloacal sucker while the pre-cloacal modification in *L. intermedia* is even more obviously sucker-like.

Family HETERAKIDAE

The family Heterakidae, as defined here, contains three distinct morphological groups. The first is characterized by (1) a short, rather stout oesophagus, (2) rather large lips, (3) interlabia (or at least structures which may be interpreted as homologous with inter-labia), (4) a rather large pre-cloacal sucker, and (5) very broad caudal alae supported by long, narrow papillae. The second is characterized by (1) rather small lips which are not set-off from the body, (2) by a relatively small pre-cloacal sucker, (3) by a flap over the vulvar opening, (4) an excretory pore which leads into a lobulate excretory vesicle and (5) by rather narrow caudal alae on the male tail which are supported by three rather small fleshy papillae. The third group is much less homogenous than the others but is characterized by (1) relatively small lips (although the anterior cuticular flange may be large) which are clearly off-set from the remainder of the body by distinct shoulders, (2) by prominent lateral lines, (3) no trace of inter-labia, (4) a relatively long, and narrow oesophagus, and (5) spicules which are always identical and relatively simple in structure. The structure of the male tail is more variable and will be discussed more fully below.

These three groups are treated as subfamilies, thus: (1) Heterakinae, (2) Meteterakinae and (3) Spinicaudinae.

Family ASPIDODERIDAE

The family Aspidoderidae consists of two distinct groups in one of which there are inter-labia modified as cordons while in the other there is no trace of inter-labia or cordons.

These two groups are treated as subfamilies: Aspidoderinae and Lauroiinae respectively.

Family ASCARIDIIDAE

The family Ascaridiidae contains only one genus, *Ascaridia*. These taxa are diagnosed formally later.

MORPHOLOGICAL AND EVOLUTIONARY TRENDS

Species of the superfamily occur in all vertebrate groups from amphibia to birds with a few representatives in mammals, except in South America where the Family Aspidoderidae is restricted to Mammals (marsupials, edentates and histricomorph rodents). In view of the great overall similarities between the component taxa it appears reasonable to consider that the superfamily represents a mono-phyletic group.

Within the family Heterakidae there is a sequence along which is a tendency towards a reduction in the number of caudal papillae, with an increase in their size and the associated appearance and increase in the size of the caudal alae. Concomitantly there is a reduction and finally a loss of the gubernaculum, an increase in the relative complexity of the spicules, an increase in the relative size of the pre-cloacal sucker and a loss of papillae on the general body surface with the development of wide lateral alae. There is also a tendency towards the development of cephalic cordons, by the modification of inter-labia associated with the lips, or by the modification of the lips alone.

That these trends have developed in the order described is supported by the host distribution of the parasites. The genera *Spinicauda*, *Africana* and *Meteterakis*, all of which are characterized by papillae on the general surface, relatively large numbers of caudal papillae, a gubernaculum or gubernacular mass, poorly developed caudal alae (when such alae are present), a relatively small pre-cloacal sucker, equal and identical spicules and no interlabia, are restricted to reptiles and amphibia.

The genera *Heterakis*, *Pseudaspidodera* and *Odonototerakis*, on the other hand, are characterized by no papillae on the body surface, relatively small numbers of elongate caudal papillae, no gubernaculum or gubernacular mass, well developed caudal alae, a relatively large pre-cloacal sucker, spicules which are frequently unequal and dissimilar and almost invariably complex, with inter-labia modified as cordons in *Pseudaspidodera* and *Odonototerakis* and are restricted, typically, to birds. Independently the genus *Gireterakis* has developed straight cordons, has no papillae on the general body surface, has very elaborate spicules and is known only from the mammal genus *Hystrix*.

It is now possible to suggest that the form ancestral to the superfamily possessed most of the following characters, although not necessarily all, (1) an anterior cuticular flange which did not project anterior to the mass of the lips; (2) no interlabia; (3) papillae on the general body surface; (4) a relatively long oesophagus with a small posterior oesophageal bulb; (5) a relatively small pre-cloacal sucker on the male tail; (6) no caudal alae on the male tail; (7) equal and identical spicules; (8) many small, sessile caudal papillae on a long, narrow male tail.

The genus *Spinicauda* possesses a combination of characters almost identical with those postulated above for an ancestral form, diverging only in that the anterior cuticular flange of the lips projects slightly anterior to the main mass of the lips, and may be considered as containing the most primitive species of the superfamily (i.e. the most generalized). Non morphological supporting evidence is given by its world-wide occurrence within tropical and subtropical regions and its restriction to reptiles. The characters of the male tail are almost identical with those

postulated for an ancestral form and as it is in just those characters that *Spinicauda* resembles the Aspidoderidae I consider the form of the male tail in that family to be relatively unspecialized.

The structure of the head in *Spinicauda* fits into an almost perfect series of increasing elaboration with *Africana*, in which the anterior cuticular flange is wholly within the limits of the lips, *Spinicauda* in which the flanges projects slightly anterior to the main mass of the lips and *Strongyluris* where the flange forms the major part of the lips and dominates the lip-mass completely (Inglis, 1957). It may be pointed out that *Africana* is a close rival to *Spinicauda* for the position of the most primitive genus and may be so considered without affecting the argument presented here.

The connection between the genera *Spinicauda* and *Strongyluris* is accentuated by the forms referred to the genus *Moaciria* (formerly treated as a subgenus of *Spinicauda*). In this latter genus the male tail is intermediate in form between the long narrow tail of *Spinicauda* and the truncate tail, with broad alae, of *Strongyluris*. This transitional form of the male tail is associated with a head which is identical in structure with that of *Spinicauda*.

The genus *Africana* appears to be atypical in being the only genus of the superfamily in which the caudal alae are not supported by caudal papillae, although this could be interpreted as an intermediate stage between the forms without alae and those with alae supported by papillae. The similarities between *Spinicauda*, *Africana*, *Moaciria* and *Strongyluris* are so great and, in addition, can be arranged in such a distinct morphological sequence with fairly clear intermediates culminating in the specialized form of *Strongyluris* that they are treated as a second evolutionary sequence recognized as the subfamily Spinicaudinae.

The remainder of the family Heterakidae falls into two distinct groups, recognized as subfamilies, Heterakinae and Meteterakinae, of which the latter appears to be the result of radiation within a restricted geographical area. The species referred to *Meteterakis* may be considered more primitive than that in *Gireterakis* in possessing a gubernacular mass and in having papillae in the general body surface. *M. triaculeatus* without a gubernacular mass being to that extent intermediate between the two genera.

The subfamily Heterakinae contains the species which are parasitic in birds and are the most highly evolved parasites, morphologically, within the family. Representatives of the subfamily occur in ground feeding, grain-eating birds throughout the world but have become sufficiently distinct in two geographical regions to warrant the recognition of two genera, *Odontoterakis* in South American tinamous and *Pseudaspidodera* in Indian peafowls. The inclusion of *Pseudaspidodera* within the Family Aspidoderidae by Skrjabin *et al.* 1961 is completely unacceptable since not only does it differ from the typical aspidoderids in the structure of the head (Inglis, 1957) but also differs in the form of the male tail with its broad, typically heterakid caudal alae, and the form of the dissimilar spicules. The resemblance must in fact be dismissed as the crudest and most superficial convergence of one morphological feature and if *Pseudaspidodera* is grouped with the aspidoderids so must the genus *Odontoterakis*, which Skrjabin *et al.* do not do.

It is also worth noting that the species referred to the genus *Heterakis* fall into two groups characterized by the structure of the spicules. The groups are not those in which the spicules are equal or unequal (as recognized by many authors, López-Néyra (1947), Skrjabin & Schikhobalova (1947), Freitas (1956) and most recently Skrjabin *et al.* (1961)), but are based on whether the spicules are identical in gross structure although they can be of different lengths (e.i. non-alate without elaborate tips) or are dissimilar (i.e. one, the left, usually bears broad alae and has an elaborate tip while the right is simple and needle-like). This difference is also geographic since the first group is most frequent in the Americas while the other is most characteristic of the European and Asiatic parasites. This difference is also reflected by the structure of the spicules in the neotropical genus *Odontoterakis*, in which the spicules are never alate and never have elaborate tips. The oriental genus *Pseudaspidodera* in contrast is characterized by dissimilar spicules in which the left spicule bears broad alae while the right is needle-like.

The family Aspidoderidae represents the radiation of a stock isolated in South American mammals. In this group most of the diversity is confined to the anterior end of the body, and superficially parallels the conditions in *Pseudaspidodera* and *Odontoterakis* but there are marked differences in the details. Thus, in the heterakids the cordons, when present, never remain the same width throughout their length even when they anastomose (accepting that they do anastomose in *Pseudaspidodera spinosa*, see below). In the family Aspidoderidae the cordons always remain the same width along their full length.

The Aspidoderidae appear to have divided into two lines: one in which inter-labia modified as cordons are present and one in which inter-labia have not appeared. Whether the species referred to *Lauroia* have been derived from the forms grouped in *Paraspidodera* is an open question but in view of the similarities of the head structures the two genera are classified in the same subfamily, Lauroiinae.

The genus *Ascaridia* is clearly heterakoid in affinity but appears to represent a group which diverged fairly early and probably shows its greatest affinities to the Spinicaudinae.

GEOGRAPHICAL AND HOST DISTRIBUTION

The superfamily as a whole is cosmopolitan in distribution and occurs in all vertebrate hosts groups from amphibia to mammals and birds, but it is in the latter group that it is most frequent and wide-spread. The distribution of the major subdivisions of the superfamily is interesting since it reflects a combination of host and geographical restrictions. Thus, the subfamily Spinicaudinae is cosmopolitan with forms occurring in all major geographical regions although restricted to reptiles and amphibia. Even the genera within the subfamily tend to be wide-spread. *Spinicauda* occurs in South America, Africa, Madagascar and Australia, with one species in each area, while *Strongyluris* is extremely widely spread in tropical and subtropical regions and is represented by a much larger number of species. In contrast *Africana* is restricted to Africa, and *Moaciria* to South America, Africa and Madagascar. *Strongyluris* appears to represent the culmination of the Spinicaudinae

and is as successful as a group of parasites in reptiles as the genus *Heterakis* is in birds.

The subfamily Heterakinae is equally wide-spread but is largely restricted to ground-feeding, grain-eating birds i.e. Galliformes (one species in mammals; *H. spalacis* and *H. macrospiculum* are not typical of the genus *Heterakis* and are best considered *incertae sedis* although the latter shows similarities to *Africana*, particularly in the structure of the male tail and spicules.) The genus *Heterakis* is cosmopolitan and ubiquitous but the other genera of the subfamily are geographically restricted with *Odontoterakis* in South America and *Pseudaspidodera* in the Indian region.

The family Aspidoderidae is the only group of the superfamily which occurs widely in mammals and it also is geographically restricted to South America while *Ascaridia*, although cosmopolitan, is most commonly reported from members of the Columbigiformes and Psittaciformes although it is not uncommon in the Galliformes.

The patterns suggest that the evolution of the superfamily has been due to a combination of (1) intra-host restriction to the caecum, (2) host restriction to ground-feeding grain-eating birds and (3) geographical restriction. There is no evidence to suggest any close host : parasite parallelism. The impression is rather of a group which has evolved and expanded to occupy all the space available to it within the constraints of the ecology and feeding habits of the hosts (see Inglis, 1965b).

Thus the members of the superfamily exist in a specialized, selected, locality within the host, in all birds in which they occur. But they only occur in a restricted range of hosts with similar feeding habits. Then the various smaller taxa are largely determined geographically. Nevertheless the Aspidoderidae represent a special case in that they are not only geographically isolated but also occur in a long isolated group of mammalian hosts, the South American marsupials and the ground-feeding edentates. It should be noted that they do not occur in the ant-eaters or the tree-dwelling sloths. It is interesting to wonder, although impossible to know, if they *continue* to exist in South America because there is no competition with other nematode parasites in the large intestine where they occur or whether they represent a new group of parasites which has replaced some other group. In other words are they a remnant group or are they the result of a specialized radiation within an isolated geographical and host locality?

Be that as it may the Heterakoidea is clearly an old group which is supremely successful within the hosts groups in which it occurs.

SYSTEMATIC HISTORY

Railliet and Henry (1914) considered that the species of the family Ascaridae for which they had created a new subfamily Heterakinae in 1912 were sufficiently distinct to warrant their further separation into a distinct family, Heterakidae. This family was diagnosed largely on the presence of a pre-cloacal sucker on the male tail and included the genera *Heterakis*, *Ascaridia*, *Aspidodera*, *Cissophylus* and *Subulura*, with *Strongyluris* as a subgenus of *Heterakis* and *Oxynema* as a subgenus of *Subulura*. No groupings higher than genera were proposed.

Travassos (1920) introduced two new genera, *Spinicauda* and *Africana*, and later in the same year (Travassos, 1920a) he divided the family Heterakidae into three subfamilies: Heterakinae, with *Heterakis*, *Ganguleterakis*, *Aspidodera*, *Paraspidodera* and *Gireterakis*; Spinicaudinae nov. for *Spinicauda*, *Africana* and *Strongyluris*; Subulurinae for *Subulura*, *Heteroxynema*, *Oxynema* and *Numidica*. The last subfamily differed from both the others in having in the males an elongate pre-cloacal sucker without a definite rim while the other two had a pre-cloacal sucker with a definite cuticular rim. The diagnostic differences between the other two subfamilies were vague and appear to have been mainly the restriction of the species of the first to warm-blooded hosts and those of the second to cold-blooded hosts.

Yorke & Maplestone (1926) considered the subfamily Subulurinae a family and did not recognize the subfamily Spinicaudinae, thus leaving the family Heterakidae with no groups higher than genera. Baylis & Daubney, slightly later in the same year (1926), still treated the subulurids as a subfamily but this was not generally accepted.

No further radical changes were proposed in the classification of the Heterakidae until Skrjabin and Schikhobalova (1947) recognized two subfamilies: Heterakinae and Aspidoderinae nov. This grouping was largely based on published descriptions and the subfamilies were considered distinct almost wholly on the presence or absence of cephalic cordons. In 1957 I described the comparative anatomy of the head in the family and argued that the classification of Skrjabin and Schikhobalova was unnatural because cephalic cordons appeared to have been developed independently three times. I then proposed that the genera *Aspidodera*, *Ansiruptodera*, *Sexansodera* and *Paraspidodera* be placed in a separate family, Aspidoderidae with two subfamilies: Aspidoderinae for the first three of the above genera and Paraspidoderinae nov. for the fourth.

Independently Freitas (1956) reviewed the family and proposed four new families, four new subfamilies and five new genera (four with one species each and one with two species). This classification was, and still is, unacceptable. There are five families of which two have only one species, there are eight subfamilies of which three have only one genus each, there are twenty-two genera of which eleven have only one species each and four have only two species each. This classification was based largely on published descriptions and every error of observation and every faulty description appears to have been recognized by a distinct genus, at least, and in some cases a subfamily or even family.

Then Chabaud (1957), in considering the classification of the suborder Ascaridina introduced a new superfamily Heterakoidea which he considered to contain two families and four subfamilies thus: Heterakidae, with four subfamilies Heterakinae (with sixteen genera or subgenera), Aspidoderinae (with four genera or subgenera), Lauroiinae (with one genus) and Schneidernematinae (with one genus); and the family Ascaridiidae with one genus, *Ascaridia*. This classification is largely that of Inglis (1957) and Freitas (1956) re-arranged.

In 1958 I proposed the classification which I am justifying here and will not discuss it now except to draw attention to the fact that *Schneidernema* and *Morgascaridia* (a genus I proposed for *Paraspidodera sellsi*, Morgan, 1928: Inglis, 1958b) were

removed from the Heterakidae first to the Ascaridiidae (Inglis, 1958b) and later to the Superfamily Seuratoidea (Inglis & Chabaud, 1958) as members of a distinct sub-family Schneidernematinae.

Most recently Skrjabin, Schikhobalova & Lagodovskaja (1961) have presented a re-arrangement of the Heterakoidea, with four families, thus: Heterakidae: Heterakinae (*Heterakis*, *Ganguleterakis* and *Odontoterakis*); Meteterakinae (*Meteterakis*; and *Gireterakis*).

Aspidoderidae: Aspidoderinae (*Aspidodera*, *Ansirutodera* and *Sexansodera*)
Spinaspiderinae (*Spinaspiderodera* and *Pseudaspiderodera*).

Spinicaudidae: Spinicaudinae (*Spinicauda*, *Africana* and *Paraspiderodera*); Preterakinae (*Preterakis*).

Strongyluridae: Strongylurinae (*Strongyluris* and *Moaciria*).

In addition they refer *Lauroia* to a distinct family within the Cosmocercoidea and introduce a new genus, *Bellapectana* for *Apectana pharyngeodentata* Belle, 1957.

It should, perhaps, be pointed out that Yamaguti (1961) has grouped the Heterakoidea in yet another way but this does not warrant serious consideration except to dismiss the new genus *Cheloniheterakis*. This genus was introduced for two old and inadequately described species from *Testudo*. No other heterakids are known from this host genus in which members of the family Kathlaniidae are fairly common parasites. As the two species referred to *Cheloniheterakis* possess circular preloacal suckers, which are common in Kathlaniids it is more probable they are referable to that family. Be that as it may the two species are *species dubia* and the genus must be ignored as unrecognizable.

The Skrjabin *et al.* classification does warrant consideration and I will give my arguments against accepting it. Part of it can be dismissed quickly and easily as due to classifying errors of description. The arguments against the genus *Bellapectana* have been adumbrated at the beginning of this paper but to recapitulate briefly the so-called teeth in the head, upon which the genus is based, do not exist they are simply the retracted lips in poorly fixed specimens. The genus *Preterakis* and the associated subfamily Preterakinae must disappear since the fusion of the caudal alae on the ventral surface of the male body is a fixation artefact and does not occur in all the specimens of the type series. The remaining arguments are more expressions of opinion and of assessing the weight of the morphological and other evidence, thus:

The reference of the aspidoderids and *Pseudaspiderodera* to the same family is a continuation of the position taken by Skrjabin & Schikhobalova (1947) but is still un-acceptable and morphologically indefensible. If this grouping is advocated there is no real reason for not referring *Odontoterakis* to the same family, but this genus is referred by Skrjabin *et al.* (1961) to the Heterakidae. I stress, and repeat what I wrote before, the only resemblance between the Aspidoderidae and *Pseudaspiderodera* is in the common possession of structures called by the same name, i.e. cordons. The family Aspidoderidae (sensu Skrjabin *et al.*) is otherwise characterized (in addition to cordons) by the presence of a cephalic cap, inter-connecting lobes to the lips, a long slim oesophagus and, in the male, is further characterized by equal and identical square-ended spicules, no caudal alae and the presence of many sessile

papillae. In all these respects *Pseudaspidodera* differs from the Aspidoderids and in all the corresponding features is identical with the genera referred by Skrjabin *et al.* to the subfamily Heterakinae.

Equally the reference of *Paraspidodera* to the Spinicaudinae is unacceptable since its only resemblance to the other genera of that subfamily is in lacking caudal alae and cephalic cordons. In all other respects, the structure of the head, the oesophagus, and the male's tail and spicules it is indistinguishable from the forms referred to the Aspidoderidae. The reference of *Lauroia* to the superfamily Cosmoceroidea is equally contradicted by the morphology. The structure of the anterior end of the body is very similar to that of the Aspidoderidae and the remnants of a pre-cloacal sucker are clearly present in at least two species.

The separation of *Strongyluris* and *Moaciria* (which I now accept as a distinct genus) into a separate family is equally unacceptable since *Strongyluris* so clearly represents the end of a morphological sequence running from *Spinicauda* to *Moaciria* to *Strongyluris*. The structure of the head in *Moaciria* is identical with that in *Spinicauda* while the male tail forms an almost perfect intermediate between that genus and *Strongyluris*.

I therefore propose the following classification for the Superfamily Heterakoidea.

ANNOTATED CLASSIFICATION OF THE SUPERFAMILY

On the basis of the arguments presented above the following classification is proposed. Notes are appended to each group to draw attention to points of interest and to explain some of the names used. In these notes some of the argument given above is briefly repeated so that this section is more or less complete in itself.

HETERAKOIDEA (Ralliet & Henry, 1912) Chabaud, 1957

Ascaridida : three large distinct lips, one dorsal with two double papillae, two ventral with a double ventral papilla and a single lateral papilla each : lining of mouth cavity (i.e. cheilorhabdion) sclerotized and forming a flange along the anterior edge of each lip in all forms except *Ascaridia* ; anterior end of oesophagus divided into three projecting lobes, one to each lip, except in *Ascaridia* ; nuclei of ventral oesophageal glands double ; no intestinal or oesophageal appendices.

MALE : circular pre-cloacal sucker with a definite cuticular rim ; two spicules.

FEMALE : eggs not embryonate *in utero*, thick-shelled ; vulva opening about middle of body.

LIFE HISTORY : Direct, with or without a migration within the final host.

HOSTS : Restricted to the intestine (more specifically to the caecum in birds and the large intestine in mammals) of ground feeding birds and mammals. In amphibia (anurans) and reptiles (saurians) restricted to terrestrial feeders.

GEOGRAPHICAL DISTRIBUTION : Cosmopolitan as a superfamily.

HETERAKIDAE Railliet & Henry, 1912

Heterakoidea : lips rounded, not connected by lateral lobes ; cordons when present poorly developed and not remaining the same width throughout their length ; oesophagus relatively short and stout.

MALES : caudal alae typically present ; number of caudal papillae relatively low ; spicules may be unequal and dissimilar ; gubernaculum generally reduced or absent ; tail generally relatively short.

HOSTS : amphibia, reptiles and (mainly) birds. One species in mammals.

DISTRIBUTION : Cosmopolitan as a family.

TYPE GENUS : *Heterakis* Dujardin, 1845.

HETERAKINAE Railliet & Henry, 1912

Heterakidae : lips not off-set from body ; anterior cuticular flange of lips generally not projecting beyond main lip mass ; inter-labia, or their homologues, present.

MALE : precloacal sucker relatively large ; caudal alae broad, supported by long, narrow papillae ; gubernaculum lacking ; spicules frequently dissimilar.

HOSTS : mainly birds, one exceptional species in mammals (rodents).

DISTRIBUTION : Cosmopolitan.

The subfamily is a homogeneous group in which three subgroups can be recognized. *Odontoterakis* is South America, *Pseudaspidodera* in India and *Heterakis* which is cosmopolitan. The latter genus is characterized by lacking definite cephalic cordons such as characterize the other two genera. But there is a tendency for there to be marked " bumps " in the inter-labial spaces which may be considered as precursors of the inter-labia which are modified as cordons in the other two genera. It is worth pointing out that what are here called cordons are identical in form and origin with the so-called labial grooves of some members of the Ascarioidea, e.g. *Porrocaecum* and *Multicaecum*. These labial grooves are also formed from two sources, one the inter-labia and the other the lips, and also consist of open grooves.

The morphological differences between *Pseudaspidodera* and *Odontoterakis* tend to be slight but in the former genus, in addition to the cordons being more strongly developed, the left spicule is always shorter than the right, is always broadly alate while the right is slim and needle-like, and generally has an elaborate posterior tip. In contrast the spicules in *Odontoterakis* are always identical in structure, never bear alae, and always end posteriorly in simple points.

I therefore interpret the two groups as having developed in specialized host groups within isolated geographical areas since *Pseudaspidodera* appears to have arisen in peafowls in India and *Odontoterakis* to have arisen in tinamous in South America. Both host groups being typically ground dwelling forms with poor powers of locomotion.

Heterakis Dujardin, 1845

Heterakinae : lips without definite inter-labia or cordons.

MALES : spicules frequently dissimilar but may be equal and identical.

TYPE SPECIES : *Ascaris gallinarum* Schrank, 1788.

HOST AND GEOGRAPHICAL DISTRIBUTION : ground feeding birds, mainly Galliformes, throughout the world.

Several attempts have been made to divide this genus into two on the basis of the relative lengths of the spicules, species with equal spicules to one genus and with unequal to another. Both López-Néyra (1947) and Skrjabin & Schikhobalova (1947a) independently attempted to do this, using the name *Ganguleterakis* for species with equal spicules. Madsen (1950), in a generally excellent and outstanding publication, commented upon this unfavourably pointing out the great difficulty in many cases in deciding whether the spicules should be called equal or unequal. Freitas (1956) attempted to over-come this difficulty by defining his two subgenera, *Heterakis* and *Raillietakis*, so that unequal spicules were considered to be those in which the difference in length was at least one third the length of the shorter spicules. Even with this qualification it is difficult to imagine that equality or its lack is a sufficiently fundamental character upon which to recognize genera or subgenera.

Skrjabin *et al.* (1961) continue to recognize two groups on just this difference in the lengths of the spicules but it is still unacceptable. It is so very clearly a bibliographical key character resorted to in an attempt to reduce the number of species within each genus and can only have been used because it is one of the few characters which can be determined from literature rather than specimens.

The structure and relative lengths of the spicules, nevertheless afford good characters in the delimitation of species within the genus used in conjunction with the number of caudal papillae, the relative size and position of the pre-cloacal sucker and the relative length of the male tail. Many authors have laid stress on the position of various caudal papillae, e.g. the number of pre-cloacal papillae, but as Maplestone (1932) and Madsen (1950), among others, have pointed out, the value of these characters is very limited.

The typical arrangement of the caudal papillae is described above but it should be noted that it is relatively common for an additional pair to occur between the para-cloaca and suctorial groups or for one of the pairs of para-cloacals to be missing. There is also a tendency, in the species occurring in South America, for a pair of long papillae to be present just anterior to the peri-cloacal group, a pair which I consider homologous with the anterior pair of peri-cloacals since in specimens on which the former pair of papillae are present the latter pair is consistently absent.

Both Maplestone (1932) and Madsen (1950) have pointed out that it is, in most cases, impossible to find characters by which the females of *Heterakis* may be distinguished. This applies throughout the entire superfamily. I have been unable to find any character, or combination of characters by which females alone can be identified.

In spite of my criticism of the attempts to divide the genus *Heterakis* on the basis

of the relative lengths of the spicules two subgroups can be recognized : (1) one in which the spicules are identical in structure and never bear alae and (2) one in which the spicules are dissimilar with the right slim and needle-like and the left broadly alate. In this latter group the posterior end of the left spicule is frequently modified into a hook or barb. In both groups the spicules may be unequal in length but in the first group when there is any modification on the posterior end it is always identical in both spicules. Thus on this basis *H. gallinarum* and *H. isolonche*, which only differ in the relative lengths of the spicules, fall together while on the basis of inequality they are completely separated.

Lane (1914) introduced the generic name *Ganguleterakis* for the species generally known as *H. spumosa* Schneider, 1866. There is a case for recognizing this genus as it contains the only species of *Heterakis* from mammals (*H. spalacis* and *H. longispiculum incertae sedis*) but, except for a reduction in the number of caudal papillae, in which it is paralleled by *H. psophiae* Travassos, 1913, it is a typical *Heterakis*. I do not, therefore, recognize this genus.

***Odontoterakis* Skrjabin & Schikhobalova, 1947a**

Heterakinae : interlabia modified as non-recurrent cordons.

MALES : spicules simple non-alate and identical in structure.

TYPE SPECIES : *Heterakis crypturi* Baylis, 1944.

HOST AND GEOGRAPHICAL DISTRIBUTION : Birds, mainly tinamous, in South America.

Note : A restudy of the types of *Heterakis interlabiata* Ortlepp, 1923 has convinced me that Mendonça (1953) is correct in treating it as a synonym of *H. isolonche*.

***Pseudaspidodera* Baylis & Daubney, 1922**

Heterakinae : inter-labia modified as recurrent cordons.

MALES : spicules dissimilar and unequal, right slim and needle-like, left with broad alae.

TYPE SPECIES : *Pseudaspidodera pavonis* Baylis & Daubney, 1922.

HOST and GEOGRAPHICAL DISTRIBUTION : Phasianid birds, India.

P. jnanendrae Chakravarty, 1938 was described as having anastomosing cordons but in the type, a female, the head is very contracted and it is probable that the apparent fusion is an artefact. *P. spinosa* Maplestone, 1932 was described as having spines in the cordons which anastomose. As a result a genus *Spinaspododera* was proposed by Skrjabin & Schikhobalova (1947) for it. There is some justification for this but in view of the small number of species involved and as Maplestone's species has never been rediscovered and the types are lost I prefer not to recognize this genus. It is worth noting that the cordons in this case, if they do definitely anastomose, vary in width along their length and do not remain the same width as in the members of the Aspidoderidae.

METETERAKINAE Inglis, 1958a

Heterakidae: head with three rounded lips, without interlabia; oesophagus relatively long with a small postoesophageal bulb; excretory pore opening into a large lobulate vesicle; lateral alae running full length of body.

MALE: spicules equal in length; caudal alae present, supported by three pairs, exceptionally four, of large fleshy papillae—one pair lateral to the cloacal opening and typically two pairs, exceptionally three, lateral to the small pre-cloacal sucker; a large number generally about twenty pairs, of small sessile papillae also present.

FEMALE: vulvar opening covered by a flap developed from the anterior lip; tail relatively very long.

TYPE GENUS: *Meteterakis* Karve, 1930.

HOST AND GEOGRAPHICAL DISTRIBUTION: Amphibia, reptiles and mammals (*Hystrix*) in the oriental region (s.l.: India, Ceylon, China, Japan, East Indies, Burma).

Meteterakis Karve, 1930

Meteterakinae: head without cordons; body generally with many small sessile papillae scattered over surface.

MALES: spicules identical; indefinite gubernacular mass developed from the walls of the cloaca—except in *M. triaculeata*; posterior lip of cloacal opening covered by small granulations.

TYPE SPECIES: *Meteterakis govindi* Karve, 1930.

HOST AND GEOGRAPHICAL DISTRIBUTION: amphibia and reptiles, as for sub-family.

Gireterakis Lane, 1917

Meteterakinae: anterior cuticular flange of lips not projecting anterior to main lip mass; three straight, simple cordons, one arising from each inter-labial space.

MALE: number of sessile caudal papillae relatively small; spicules elaborate; no gubernacular mass present.

TYPE SPECIES: *Gireterakis girardi* Lane, 1917.

HOST AND GEOGRAPHICAL DISTRIBUTION: *Hystrix* species in India.

SPINICAUDINAE Travassos, 1920

Heterakidae: lips off-set from body; no inter-labia or cordons; lateral fields prominent; papillae on body.

MALE: spicules equal, identical and simple; papillae do not support caudal alae when alae present except when the tail is short and the pre-cloacal sucker is directed posteriorly.

TYPE GENUS: *Spinicauda* Travassos, 1920.

HOST AND GEOGRAPHICAL DISTRIBUTION: Amphibia and reptiles; cosmopolitan in the tropics and sub-tropics.

This subfamily is morphologically the least uniform, and therefore the most difficult to diagnose, in the superfamily Heterakoidea. This is mainly because *Spinicauda* is morphologically generalized while *Strongyluris* is highly modified. A trend in the modification of the head is apparent from *Africana*, with a simple anterior cuticular flange, to *Spinicauda* and *Moaciria* in which the flange projects slightly beyond the lip mass to *Strongyluris* in which the flange forms the major part of the lip. *Moaciria* forms an almost perfect intermediate stage between *Spinicauda* and *Strongyluris* since it resembles *Spinicauda* in the presence of a gubernaculum and in having the same head form and resembles *Strongyluris* in the posteriorly directed pre-cloacal sucker and the presence of caudal alae (narrow) supported by longish papillae. I treated *Moaciria* as a subgenus of *Spinicauda* in 1958 but now prefer to treat it as a distinct genus.

Spinicauda Travassos, 1920a

Spinicaudinae : anterior cuticular flange projects slightly beyond the main mass of the lips.

MALE : tail relatively long, tapering evenly to a point ; pre-cloacal sucker relatively small ; gubernaculum present ; caudal papillae small and sessile.

TYPE SPECIES : *Ascaris spinicauda* Rudolphi, 1819.

HOST AND GEOGRAPHICAL DISTRIBUTION : Reptiles in South America, Africa, Madagascar and Australia (Queensland). i.e. tropical and subtropical.

Africana Travassos, 1920

Spinicaudinae : anterior cuticular flange not projecting anterior to lips ; lateral alae present.

MALES : pre-cloacal sucker small ; spicules equal and identical, alate ; gubernaculum present ; small sessile papillae on tail ; caudal alae not supported by papillae ; caudal alae stop about level of cloacal opening.

TYPE SPECIES : *Heterakis africana* Gendre, 1909.

HOST AND GEOGRAPHICAL DISTRIBUTION : Amphibia and reptiles in tropical and subtropical Africa.

Moaciria Freitas, 1956a

Spinicaudinae : anterior cuticular flange projecting slightly anterior to mass of lips.

MALE : tail relatively long with relatively few stoutish papillae supporting narrow caudal alae ; posteriorly directed pre-cloacal sucker ; gubernaculum present.

TYPE SPECIES : *Moaciria alvarengai* Freitas, 1956a.

HOST AND GEOGRAPHICAL DISTRIBUTION : Reptiles in South America, Africa and Madagascar.

***Strongyluris* Mueller, 1894**

Spinicaudinae : anterior cuticular flange projecting beyond main lip mass so that it forms major portion of lip ; sessile papillae scattered over body surface.

MALE : posterior end obliquely truncate ; pre-cloacal sucker relatively large and directed posteriorly ; caudal alae well developed, supported by rather long, stout caudal papillae ; spicules equal, without alae ; no gubernaculum or gubernacular mass present.

TYPE SPECIES : *Strongyluris brevicaudata* Mueller, 1894.

HOST AND GEOGRAPHICAL DISTRIBUTION : Mainly reptiles, rarely amphibians, cosmopolitan within the tropics and subtropics.

ASPIDODERIDAE Skrjabin & Schikhobalova, 1947

Heterakoidea : lips square connected by lateral lobes ; cuticle at anterior end of body thickened to form a cephalic cap ; oesophagus long and narrow with a small posterior oesophageal bulb ; cordons, when present, the same width along their lengths.

MALES : no caudal alae ; gubernaculum generally present ; spicules equal in length and identical in structure, generally massive ; generally many small sessile papillae on long, narrow tail ; caudal papillae all about the same size.

TYPE GENUS : *Aspidodera* Railliet & Henry, 1912.

HOSTS AND GEOGRAPHICAL DISTRIBUTION : Marsupials, edentates and occasionally hystricomorphs in South America and related areas.

ASPIDODERINAE Skrjabin & Schikhobalova, 1947

Aspidoderidae : cephalic cordons present, lateral lobes of lips complex.

TYPE GENUS : *Aspidodera* Railliet & Henry, 1912.

DISTRIBUTION : As family.

***Aspidodera* Railliet & Henry, 1912**

Aspidoderinae : cephalic cordons recurrent and anastomosing.

TYPE SPECIES: *Aspidodera scoleciformes* Diesing, 1851.

***Ansirutodera* Skrjabin & Schikhobalova, 1947**

Aspidoderinae : cephalic cordons not anastomosing.

TYPE SPECIES : *Aspidodera ansirutodera* Proença, 1937.

LAUROIINAE Skrjabin & Schikhobalova, 1951

Aspidoderidae : cephalic cordons lacking ; lateral lobes of lips simple.

TYPE GENUS : *Lauroia* Proença, 1938.

HOST AND GEOGRAPHICAL DISTRIBUTION : Edentates and hystricomorphs, as the family.

Lauroia Proença, 1938

Lauroiinae : cephalic cap modified into three "plates" which are slightly undercut posteriorly. This modification can be interpreted as due to the development of cordons which do not involve inter-labia as in *Gireterakis*.

MALE : posterior end simple without a gubernaculum, relatively few papillae, and a reduced pre-cloacal sucker.

TYPE SPECIES : *Lauroia travassosi* Proença, 1938.

Paraspidodera Travassos, 1914

Lauroiinae : cephalic cap not modified as "plates".

MALE : posterior end relatively complex, with a gubernaculum; relatively large number of caudal papillae and a well developed pre-cloacal sucker.

TYPE SPECIES : *Paraspidodera uncinata* Rudolphi, 1819.

ASCARIDIIDAE Travassos, 1919

Heterakoidea : lips large and stout ; no distinct anterior cuticular flange ; oesophagus club-shaped without a posterior bulb.

MALE : caudal alae narrow supported by short stout papillae.

TYPE GENUS : *Ascaridia* Dujardin, 1845.

HOST AND GEOGRAPHICAL DISTRIBUTION : Birds, cosmopolitan with rare species in mammals.

KEY TO THE GENERA OF THE SUPERFAMILY HETERAKOIDEA

- | | | | |
|------|------|--|-------------------------|
| (1) | (2) | Without a tri-valvulate posterior oesophageal bulb | ASCARIDIA (p. 24) |
| (2) | (1) | With a tri-valvulate posterior oesophageal bulb | (3) |
| (3) | (18) | Head without a cephalic cap, without interconnecting lobes to lips | (4) |
| (4) | (9) | Anterior cuticular flange of lip not projecting anterior to main lip mass, no papillae on body, lateral alae present, broad caudal alae supported by long, thin papillae | (5) |
| (5) | (6) | Head without cordons or labial grooves | HETERAKIS (p. 19) |
| (6) | (5) | Head with cordons or labial grooves | (7) |
| (7) | (8) | Spicules dissimilar, left with broad alae, right needle-like, restricted to India and associated regions. | PSEUDASPIDODERA (p. 20) |
| (8) | (7) | Spicules similar, never alate, restricted to South America | ODONTOTERAKIS (p. 20) |
| (9) | (15) | Narrow lateral alae, papillae on body surface, caudal alae when present either not supported by papillae or supported by many short, stoutish papillae | (10) |
| (10) | (11) | No caudal alae on male tail | SPINICAUDA (p. 22) |
| (11) | (12) | Caudal alae not supported by papillae | AFRICANA (p. 22) |
| (12) | (15) | Caudal alae supported by stout papillae, male tail obliquely truncate, and sucker directed posteriorly | (13) |

- (13) (14) Male tail without long terminal spike, anterior cuticular flange major part of lip STRONGYLURIS (p. 23)
- (14) (13) Male tail with long terminal spike, anterior flange not major part of lip MOACIRIA (p. 22)
- (15) (9) Caudal alae supported by 3-4 stout papillae (16)
- (16) (17) Straight cordons running posteriorly from interlabial spaces, spicules very complex GIRETERAKIS (p. 21)
- (17) (16) No cordons, spicules not very complex METETERAKIS (p. 21)
- (18) (3) Head with a cephalic cap, interconnecting lobes to lips (19)
- (19) (22) Head without cordons (20)
- (20) (21) Head with three cuticular "plates", pre-cloacal sucker reduced, or lacking LAUROIA (p. 24)
- (21) (20) Head without cuticular "plates", sucker normal PARASPIDODERA (p. 24)
- (22) (19) Head with cordons (23)
- (23) (24) Cordons not anastomosing ANSIRUPTODERA (p. 23)
- (24) (23) Cordons anastomosing ASPIDODERA (p. 23)

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APPENDIX

While this paper was in press Chabaud (Alain G.) and Dollfus (Robert Ph.) have published the description of a new genus and species of heterakid (1966, *Hatterianema hollandei* N.G., N.SP., nematode hétérakide parasite de rhynocéphale. *Bull. Mus. nat. hist. Nat.* Ser. 2, **37**: 1041-1045) which they refer to the subfamily Meteterakinae.

However, from the description the species is referable to the Spinicaudinae rather than Meteterakinae since 1) the lips appear to be offset from the body, 2) there are no caudal alae on the male tail, 3) a gubernaculum is present, 4) there is no

flap over the vulva in the female. In the key given above *H. hollandei* comes out at *Spinicauda* from which *Hatterianema* appears to differ largely in not possessing a cuticular flange projecting beyond the main mass of the lips and the large number of caudal papillae. In fact *Hatterianema* corresponds almost perfectly to the hypothetical ancestral form deduced above.

